THE INTERNATIONAL SYMPOSIUM ON THE ECOLOGY OF LARVAL MOLLUSCS: INTRODUCTION AND SUMMARY

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Working on molluscs, I am continually impressed with the potential for research on comparative larval ecology. Molluscan species fill a broad ecological spectrum from infaunal species and sedentary oysters to pelagic squids and pteropods. Included are marine, freshwater, and terrestrial forms. Not only do molluscs represent varied evolutionary backgrounds (Shuto, 1974; Scheltema, 1978; Scheltema and Williams, 1983), but their fossil record allows inferences on ancient larval ecology (e.g. Kauffman, 1975; Lutz and Jablonski, 1978; Jablonski and Lutz, 1980; Hansen, 1978; 1980; Bouchet, 1981; Powell *et al.*, 1984).

This symposium grew out of the frustration I experienced in attempting field studies of comparative larval ecology (Vecchione, 1979; Vecchione and Grant, 1983). The causes of this frustration were serious taxonomic problems and a literature base that was scattered and often difficult to obtain. Larval development has been adequately described for only a small percentage of molluscan species known to have planktonic larvae. Many of the existing descriptions are of little use for definitive identification of specimens in plankton samples. Although some very useful studies describe veligers of molluscs (e.g. Loosanoff *et al.*, 1966; Chanley and Andrews, 1971), many are unpublished theses (e.g. Taylor, 1975) or individual articles either in broad-spectrum journals (e.g. Lebour, 1937; 1945; Sullivan, 1948; Rees, 1950; Richter and Thorson, 1975; Pilkington, 1976; LePennec, 1980; Lutz *et al.*, 1982; Thiriot-Quievreux and Scheltema, 1982; Thiriot-Quievreux, 1983) or in symposia proceedings and other publications with limited distribution (e.g. Jorgensen, 1946; Thorson, 1946; Fretter and Pilkington, 1970).

Presently, the base of literature on larval studies from many diverse phyla is expanding rapidly. General questions are being defined for which tests of hypotheses will allow development of early-life-history theory (e.g. Vance, 1973; Obrebski, 1979; Jackson and Strathmann, 1981; Keough and Downes, 1982; Roughgarden *et al.*, 1985). For instance, within available resources how can a species adapt so that energy can be allocated adequately to reproduction and other functions? Is the function of a larval stage to allow dispersal and colonization, to take advantage of resources that would not be available with direct development (e.g. near-surface phytoplankton), or to minimize intra-specific competition between adults and offspring? Whatever the role of the larval stage, both benthic and pelagic species with planktonic young face the requirement of either retention within the adult habitat or recruitment to suitable areas. Determining the evolutionary solution to the retention vs. recruitment dichotomy involves elucidation of behavioral mechanisms (e.g. Mileikovsky, 1973; Richter, 1973), defining cues and responses (e.g. Cole and Knight-Jones, 1939; Scheltema, 1961; Thorson, 1966; Crisp, 1967; Hidu, 1969; Hidu and Haskins, 1971; Cragg and Gruffydd, 1975; Mann and Wolf, 1983). The choice between retention and recruitment will affect population phenomena such as gene flow (Scheltema, 1971; 1975) which, in turn, affects speciation and higher-level systematics over geological time (Jablonski, 1982; Hansen, 1983).

For species with a free-living larval stage, larval mortality may be a particularly important factor in population dynamics (Thorson, 1950). Potential sources of larval mortality currently receiving much attention include starvation (e.g. Beyer, 1980; O'Connell, 1980; Anger *et al.*, 1981), predation (e.g. Mileikovsky, 1974; Burrell and Van Engel, 1976; Steinberg and Kennedy, 1979), pollution (e.g. Roosenburg *et al.*, 1980; Wright *et al.*, 1983), and "wastage" due to transport into unfavorable areas (e.g. Smyth, 1980; Norcross and Shaw, 1984). Any of these phenomena will affect recruitment, both in the fisheries sense and in the biological sense. Thus, population size of a species may (or may not: Watzin, 1983) be strongly linked to larval ecology (Thorson, 1966).

Much of the conceptual development behind these questions is based on classical studies of larval molluscs. The problems of retention of oyster larvae within the commercial fishing grounds have received much attention (Carriker, 1951; Pritchard, 1952; Wood and Hargis, 1971; Seliger *et al.*, 1982). Scheltema's (1971) pioneering work on delay of metamorphosis, contrasting the biogeographic potential of species having teleplanic larvae with those having actaeplanic larvae, has formed the framework of studies based on many phyla (e.g. Scheltema, 1975; Laursen, 1981; Rice, 1981; Domanski, 1984). Thorson (1950) relied heavily on prosobranch gastropods to detail the overall relationship between developmental modes and latitude. Postlarval events that are a continuation of the larval history were pointed out for young

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mussels (Bayne, 1964) and still constitute a subject ripe for research (e.g. Sigurdsson *et al.*, 1976; Luckenbach, 1984; Petersen, 1984; Prezant and Chalermwat, 1984). Conversely, the possible effects of starvation and "larval wastage", which have been shown to be quite important in the life histories of species in other phyla, have been largely neglected in studies of larval molluscs (Vecchione, 1981; in press).

Although I must confess a substantial ignorance of freshwater molluscs, it seems to me that the developmental patterns unique to this group should allow interesting comparative studies, not only on larval ecology but also on the evolution of parasitism.

This symposium was organized to assemble as diverse a group of researchers as possible. Topics included distribution, physiology, behavior, and taxonomy. As many taxa and habitats were included as possible, as were both basic and applied studies. My primary goal in organizing the symposium was to get people from many backgrounds talking together.

This goal was fulfilled by a truly international assemblage of scientists. In all, 17 papers were presented, representing the work of 29 authors from seven countries. Of these papers, six are presented in their entirety in this issue. Several authors had plans to publish their work elsewhere whereas others are continuing data collection and analyses. Some of these studies are presented here as expanded abstracts.

Probably the most delightful parts of this symposium for those of us who attended were the many discussions after papers, in hallways and eating places, and during the "round-table" session that concluded the symposium. One purpose of the "round-table" was to compile a list of recommendations that participants felt were important topics for future research. The following are the recommendations proposed and agreed upon by those in attendance.

(1) *Careful systematic studies of larvae.* There was a strong consensus among the participants that thorough studies of larval taxonomy and systematics are needed and are basic to the study of larval ecology.

(2) *Postlarval transport processes.* Many participants had observed that planktonic transport of postlarval molluscs is a widespread though largely undocumented phenomenon. Potential mechanisms mentioned for such transport include "byssus-drifting", production of mucous threads for resuspension by currents, rafting on floating material, and dispersal on surface tension.

(3) *Interaction of recruitment and larval/postlarval phenomena.* Recruitment may be affected either by larval (planktonic) phenomena or by postlarval (benthic, or as in (2) above, planktonic) phenomena. Many participants felt that since the early benthic phase is actually meiofaunal in size, this phase has been inadequately investigated and specific studies should be designed using meiofaunal techniques (e.g. Muss, 1973).

(4) *Comparative studies of larval ecology.* Hypotheses about larval ecology can effectively be tested by comparative studies using sibling species with different developmental adaptations or by similar comparisons among higher taxa (e.g. Ament, 1979).

(5) *Combined laboratory and field studies.* Cross-verification is needed between observations resulting from field and laboratory studies. Empirical work in the field can develop specific questions that may be testable under controlled laboratory conditions, and laboratory experiments may serve as a useful guide for the design of field sampling programs. Such combined studies would more effectively estimate the range of potentials of which larvae are capable.

(6) *Alternate hypotheses for developmental types.* The function of the larval phase in a species' life history is often assumed (e.g. feeding vs. dispersal vs. the necessity to attain an adequate size to metamorphose or set). Tests must be designed to examine the appropriateness of such assumptions.

(7) *Genetics of poecilogony and yolk dynamics.* Is a species capable of altering its developmental pattern among planktotrophy, lecithotrophy, and direct development (Robertson, 1974) and, if so, are such alterations reversible? Current evidence on poecilogony, or developmental plasticity, ranges from equivocal to contradictory.

(8) *Assumptions of applied ecology.* Frequently, applied disciplines, such as fisheries science or pollution ecology, base predictions on assumptions about larval ecology of questionable validity. Although the participants recognized that this is often a requirement when decisions must be made and the necessary data do not exist, these assumptions should be carefully examined and, when necessary, tested.

A symposium introduction is not the proper forum for a thorough review of larval ecology. My purpose here has been simply to show that we who work with larval molluscs are building on a broad foundation. This foundation is the work of the many researchers mentioned above and many others omitted because of the constraints of an introductory overview. I hope that publication of this symposium will provide stimulus and direction for equally varied and interesting work.

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LITERATURE CITED

Ament, A. S. 1979. Geographic variation in relation to life history in three species of the marine gastropod genus *Crepidula:* Growth rates of newly hatched larvae and juveniles. In: Stancyk, S. E. (ed.) *Reproductive Ecology of Marine Invertebrates.* University of South Carolina Press. Columbia, SC. pp. 61-76.

Anger, K., R. R. Dawirs, V. Anger, and J. D. Costlow. 1981. Effects of early starvation periods on zoeal development of brachyuran crabs. *Biological Bulletin* 161:199-212.

Bayne, B. L. 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *Journal of Animal Ecology* 33:513-523.

Beyer, J. E. 1980. Feeding success of clupeoid fish larvae and stochastic thinking. *Dana* 1:65-91.

Bouchet, P. 1981. Evolution of larval development in eastern Atlantic Terebridae (Gastropoda), Neogene to Recent. *Malacologia* 21:363-369.

Burrell, V. G. and W. A. Van Engel. 1976. Predation by and distribution of a ctenophore, *Mnemiopsis leidyi* A. Agassiz, in the York River Estuary. *Estuarine and Coastal Marine Science* 4:235-242.

Carriker, M. R. 1951. Ecological observations on the distribution of oyster larvae in New Jersey estuaries. *Ecological Monographs* 21:19-38.

Chanley, P. and J. D. Andrews. 1971. Aids for the identification of bivalve larvae of Virginia. *Malacologia* 11:45-119.

Cole, H. A. and E. W. Knight-Jones. 1939. Some observations and experiments on the settling behavior of larvae of *Ostrea edulis*. *Journal du Conseil Perm. International pour l' Exploration de la Mer* 14:86-105.

Cragg, S. M. and LI. D. Gruffydd. 1975. The swimming behavior and the pressure responses of the veliconcha larvae of *Ostrea edulis* L. In: Barnes, H. (ed.) *Proceedings of the Fourth European Marine Biology Symposium*. Aberdeen University Press. pp. 43-57.

Crisp, D. J. 1967. Chemical factors inducing settlement in *Crassostrea virginica* (Gmelin). *Journal of Animal Ecology* 36:329-336.

Domanski, P. A. 1984. Giant larvae: prolonged planktonic larval phase in the asteroid *Luidia sarsi*. *Marine Biology* 80:189-195.

Fretter, V. and M. C. Pilkington. 1970. Prosobranchia — veliger larvae of Taenioglossa and Stenoglossa. *Zooplankton Sheets* 129-132. Consiel International pour l' Exploration de la Mer. 26 pp.

Hansen, T. A. 1978. Larval dispersal and species longevity in Lower Tertiary gastropods. *Science* 199:885-887.

Hansen, T. A. 1980. Influence of larval dispersal and geographic distribution on species longevity in neogastropods. *Paleobiology* 6:193-207.

Hansen, T. A. 1983. Modes of larval development and rates of speciation in early Tertiary neogastropods. *Science* 220:501-502.

Hidu, H. 1969. Gregarious setting in the American oyster, *Crassostrea virginica*. *Chesapeake Science* 10:85-92.

Hidu, H. and H. H. Haskins. 1971. Setting of the American oyster related to environmental factors and larval behavior. *Proceedings of the National Shellfish Association* 61:35-50.

Jablonski, D. 1982. Evolutionary rates and modes in Late Cretaceous gastropods: role of larval ecology. *Third North American Paleontological Convention Proceedings*, Vol. I, pp. 257-262.

Jablonski, D. and R. A. Lutz. 1980. Molluscan larval shell morphology — ecological and paleontological applications. In: Rhodes, D. C. and R. A. Lutz (eds.) *Skeletal Growth of Aquatic Organisms*. Plenum Press, New York, NY. pp. 323-377.

Jackson, G. A. and R. R. Strathmann. 1981. Larval mortality from offshore mixing as a link between precompetent and competent periods of development. *American Naturalist* 118:16-26.

Jorgensen, C. B. 1946. Lamellibranchia. *Meddelelser Komm. Danmarks Fiskfri-og Havundersogelser, Ser. Plankton* 4:277-311.

Kauffman, E. G. 1975. Dispersal and biostratigraphic potential of Cretaceous benthonic Bivalvia in the Western Interior. *Geological Association of Canada Special Paper* 14:163-194.

Keough, M. J. and B. J. Downes. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia* 54:348-352.

Laursen, D. 1981. Taxonomy and distribution of teleplanic prosobranch larvae in the North Atlantic. *Dana Report* 89:1-44.

Lebour, M. V. 1937. The eggs and larvae of the British prosobranchs with special reference to those living in the plankton. *Journal of the Marine Biological Association of the United Kingdom* 22:105-166.

Lebour, M. V. 1945. The eggs and larvae of some prosobranchs from Bermuda. *Proceedings of the Zoological Society of London* 114:462-489.

Le Pennec, M. 1980. The larval and post-larval hinge of some families of bivalve molluscs. *Journal of the Marine Biological Association of the United Kingdom* 60:601-617.

Loosanoff, V. L., H. C. Davis, and P. E. Chanley. 1966. Dimensions and shapes of some marine bivalve mollusks. *Malacologia* 4:351-435.

Luckenbach, M. W. 1984. Settlement and early post-settlement survival in the recruitment of *Mulinia lateralis* (Bivalvia). *Marine Ecology — Progress Series* 17:245-250.

Lutz, R., J. Goodell, M. Castagna, S. Chapman, C. Newell, H. Hidu, R. Mann, D. Jablonski, V. Kennedy, S. Sidell, R. Goldberg, H. Beattii, C. Falmagne, A. Chestnut, and A. Partridge. 1982. Preliminary observations on the usefulness of hinge structure for identification of bivalve larve. *Journal of Shellfish Research* 2:65-70.

Lutz, R. A. and D. Jablonski. 1978. Larval bivalve shell morphometry: A new paleoclimatic tool? *Science* 202:51-53.

Mann, R. and C. C. Wolf. 1983. Swimming behavior of larvae of the ocean quahog *Arctica islandica* in response to pressure and temperature. *Marine Ecology — Progress Series* 3:211-218.

Mileikovsky, S. A. 1973. Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. *Marine Biology* 23:11-18.

Mileikovsky, S. A. 1974. On predation of pelagic larvae and early juveniles of marine bottom invertebrates and their passing alive through their predators. *Marine Biology* 26:303-311.

Muss, K. 1973. Settling, growth and mortality of young bivalves in the Oresund. *Ophelia* 12:79-116.

Norcross, B. L. and R. F. Shaw. 1984. Oceanic and estuarine transport of fish eggs and larvae: A review. *Transactions of the American Fisheries Society* 113:153-165.

Obrebski, S. 1979. Larval colonizing strategies in marine benthic invertebrates. *Marine Ecology — Process Series* 1:293-300.

O'Connell, C. P. 1980. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. *Fishery Bulletin* 78:475-489.

Petersen, J. H. 1984. Establishment of mussel beds: Attachment behavior and distribution of recently settled mussels (*Mytilus californiensis*). *Veliger* 27:7-13.

Pilkington, M. C. 1976. Descriptions of veliger larvae of monocaridan gastropods occurring in Otago plankton hauls. *Journal of Molluscan Studies* 42:337-360.

Powell, E. N., H. Cummins, R. J. Stanton, and G. Staff. 1984. Estimation of the size of molluscan larval settlement using the death assemblage. *Estuarine, Coastal, and Shelf Science* 18:367-384.

Prezant, R. S. and K. Chalermwat. 1984. Flotation of the bivalve *Corbicula fluminea* as a means of dispersal. *Science* 225:1491-1493.

Pritchard, D. W. 1952. Distribution of oyster larvae in relation to hydrographic conditions. *Proceedings of the Gulf and Caribbean Fisheries Institute* 5:123-132.

Rees, C. B. 1950. The identification and classification of lamellibranch larvae. *Hull Bulletin of Marine Ecology* 3:73-104.

Rice, M. E. 1981. Larvae adrift: Patterns and problems in life histories

of sipunculans. *American Zoologist* 21:605-619.

Richter, G. 1973. Field and laboratory observations on the diurnal vertical migration of marine gastropod larvae. *Netherlands Journal of Sea Research* 7:126-134.

Richter, G. and G. Thorson. 1975. Pelagische Prosobranchier larven des Golfes von Neapel. *Ophelia* 13:109-185.

Robertson, R. 1974. Marine prosobranch gastropods: larval studies and systematics. *Thalassia Jugoslavica* 10:213-238.

Roosenburg, W. H. , J. C. Rhoderick, J. M. Block, V. S. Kennedy, S. R. Gullans, S. M. Vreenegoor, A. Rosenkranz, and C. Collette. 1980. Effects of chlorine-produced oxidants on survival of larvae of the oyster *Crassostrea virginica*. *Marine Ecology — Progress Series* 3:93-96.

Roughgarden, J., Y. Iwasa, and C. Baxter. 1985. Demographic theory for an open marine population with space-limited recruitment. *Ecology* 66:54-67.

Scheltema, R. S. 1961. Metamorphosis of the veliger larvae of *Nassarius obsoletus* (Gastropoda) in response to bottom sediment. *Biological Bulletin* 120:92-109.

Scheltema, R. S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biological Bulletin* 140:284-322.

Scheltema, R. S. 1975. The relationship of larval dispersal, gene flow and natural selection to geographical variation of benthic invertebrates in estuaries and coastal regions. In: Cronin, L. E. (ed.) *Estuarine Research, Volume 1. Chemistry, Biology and the Estuarine System.* Academic Press. New York, NY. pp. 322-391.

Scheltema, R. S. 1978. On the relationship between the dispersal of pelagic veliger larvae and the evolution of marine prosobranch gastropods. In: Brattaglia, B. and J. A. Beardmore (eds.) *Marine Organisms — Genetics, Ecology, and Evolution.* Plenum Press. New York, NY. pp. 303-322.

Scheltema, R. S. and I. P. Williams. 1983. Long-distance dispersal of planktonic larvae and the biology and evolution of some Polynesian and western Pacific mollusks. *Bulletin of Marine Science* 33:545-565.

Seliger, H. H., J. A. Boggs, R. B. Rivkin, W. H. Biggley, and K. R. H. Aspden. 1982. The transport of oyster larvae in an estuary. *Marine Biology* 71:57-72.

Shuto, T. 1974. Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. *Lethaia* 7:239-256.

Sigurdsson, J. B., C. W. Titman, and P. A. Davies. 1976. The dispersal of young post-larval bivalve molluscs by byssus threads. *Nature* 262:386-387.

Smyth, P. O. 1980. *Callinectes* (Decapoda: Portunidae) larvae in the Middle Atlantic Bight, 1975-77. *Fishery Bulletin* 78:251-265.

Steinberg, P. D. and V. S. Kennedy. 1979. Predation upon *Crassostrea virginica* (Gmelin) larvae by two invertebrate species common to Chesapeake Bay oyster bars. *Veliger* 22:78-84.

Sullivan, C. M. 1948. Bivalve Larvae of Malpeque Bay, P. E. I. *Bulletin of the Fisheries Research Board of Canada* 77:1-36.

Taylor, J. B. 1975. Planktonic prosobranch veligers of Kaneohe Bay. Ph.D. Dissertation, University of Hawaii. 593 pp.

Thiriot-Quievreux, C. 1983. Summer meroplanktonic prosobranch larvae occurring off Beaufort, North Carolina. *Estuaries* 6:387-398.

Thiriot-Quievreux, C. and R. S. Scheltema. 1982. Pelagic larvae of New England gastropods. V. *Bittium alternatum, Triphora nigrocincta, Cirithiopsis emersoni, Lunatia heros,* and *Crepidula plana. Malacologia* 23:37-46.

Thorson, G. 1946. Reproduction and larval ecology of Danish marine bottom invertebrates. *Meddelelser Komm. Danmarks Fiskfri-og Havundersogelser, Ser. Plankton* 4:1-523.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews* 25:1-45.

Thorson, G. 1966. Some factors influencing the recruitment of marine benthic communities. *Netherlands Journal of Sea Research* 3:267-293.

Vance, R. R. 1973. On reproductive strategies in marine benthic invertebrates. *American Naturalist* 107:339-352.

Vecchione, M. 1979. Planktonic molluscan faunal structure across a large scale environmental gradient. Ph.D. Dissertation, College of William and Mary. 158 pp.

Vecchione, M. 1981. Aspects of the early life history of *Loligo pealei* (Cephalopoda; Myopsida). *Journal of Shellfish Research* 1:171-180.

Vecchione, M. in press. The ecology of juvenile cephalopods. In: Boyle, P. (ed.) *Cephalopod Life Cycles, Volume* 2. Academic Press, New York, NY.

Vecchione, M. and G. C. Grant. 1983. A multivariate analysis of planktonic molluscan distribution in the Middle Atlantic Bight. *Continental Shelf Research* 1:405-424.

Watzin, M. C. 1983. The effect of meiofauna on settling macrofauna: meiofauna may structure macrofaunal communities. *Oecologia* 59:163-166.

Wood, L. and W. J. Hargis. 1971. Factors associated with the transport and retention of bivalve larvae in a tidal estuary. In: Crisp, D. J. (ed.) *Fourth European Marine Biological Symposium.* Cambridge University Press. pp. 29-44.

Wright, D. A., V. S. Kennedy, W. H. Roosenburg, M. Castagna, and J. A. Mihursky. 1983. Temperature tolerance of embryos and larvae of five bivalve species under simulated power plant entrainment conditions: a synthesis. *Marine Biology* 77:271-278.